Perceptual reversals in binocular rivalry: Improved detection from OKN

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When binocular rivalry is induced by opponent motion displays, perceptual reversals are often associated with changed oculomotor behavior (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014; Fujiwara et al., 2017). Specifically, the direction of smooth pursuit phases in optokinetic nystagmus typically corresponds to the direction of motion that dominates perceptual appearance at any given time. Here we report an improved analysis that continuously estimates perceived motion in terms of “cumulative smooth pursuit.” In essence, smooth pursuit segments are identified, interpolated where necessary, and joined probabilistically into a continuous record of cumulative smooth pursuit (i.e., probability of eye position disregarding blinks, saccades, signal losses, and artefacts). The analysis is fully automated and robust in healthy, developmental, and patient populations. To validate reliability, we compare volitional reports of perceptual reversals in rivalry displays, and of physical reversals in nonrivalrous control displays. Cumulative smooth pursuit detects physical reversals and estimates eye velocity more accurately than existing methods do (Frässle et al., 2014). It also appears to distinguish dominant and transitional perceptual states, detecting changes with a precision of ±100 ms. We conclude that cumulative smooth pursuit significantly improves the monitoring of binocular rivalry by means of recording optokinetic nystagmus.

Introduction

Studies of binocular rivalry typically rely on volitional reports from observers trained to communicate their subjective perceptual experience as rapidly and faithfully as possible (Logothetis, Leopold, & Sheinberg, 1996; Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006; Sterzer, Kleinschmidt, & Rees, 2009). Although subjective reports are perfectly adequate for numerous research questions, they suffer from certain limitations. For example, volitional reports cannot be produced repeatedly at short intervals (< 200 ms), the underlying subjective criteria are difficult to establish, volitional reports require...
cooperative and healthy observers to be informative, and they necessitate additional neural activity, contaminating any activity associated with perceptual reversals.

An alternative to volitional reports are so-called “no-report” paradigms, which seek to monitor perceptual state on the basis of objective behavioral or physiological measures (Tsuchiya, Wilke, Frässle, & Lamme, 2015; Overgaard & Fazekas, 2016). The most established no-report paradigm relies on optokinetic nystagmus (OKN), but modulation of pupil diameter and entrainment of physiological responses by frequency- or contrast-tagged displays (EEGs) have also been widely used (Lansing, 1964; Brown & Norcia, 1997; Tononi, Srinivasan, Russell, & Edelman, 1998; Kornmeier & Bach, 2005; Kamphuisen, Bauer, & van Ee, 2008; Kornmeier & Bach, 2012; Jamison, Roy, He, Engle, & He, 2015).

It has long been understood that OKN can reveal subjective perceptual experience, provided that the rivalrous displays are designed to elicit antagonistic nystagmus responses (Enoksson, 1963; Fox, Todd, & Bettinger, 1975). For example, if translational motion to the left and right is presented dichoptically to both eyes, the smooth pursuit phases of OKN will typically follow the perceptually dominant motion. When perceptual dominance reverses, the direction of smooth pursuit typically reverses as well. The validity of this approach was confirmed with magnetic scleral coils both in non-human primates trained to report their subjective experience and in human observers (Logothetis & Schall, 1990; Wei & Sun, 1998) and was subsequently extended to infrared eye trackers (Watanabe, 1999; Naber, Frässle, & Einhäuser, 2011; Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014).

Typically, the recorded eye velocity is processed and filtered to extract the slow (“pursuit”) phase of OKN (Naber et al., 2011; Frässle et al., 2014; Fujiwara et al., 2017), and slow velocity is categorized in a binary fashion, such as to identify periods with a consistent direction of perceived motion (“dominance periods”). While this approach reliably identifies long dominance periods, shorter periods of either dominance or transition are more difficult to resolve.

Here we report an improved analysis that yields a continuous record of “cumulative smooth pursuit” (CSP). This record consists of a sequence of eye velocity estimates (with confidence limits), which seamlessly joins pursuit periods and interpolated periods. The sequence of velocity estimates can be parsed into distinct phases of “pursuit dominance” (with a typical mean duration ~2 s) and “pursuit transitions” (typical duration ~0.25 to ~0.5 s). The change-over between phases can be determined with a precision of approximately ±100 ms.

The analysis is robust and enables studies with large and diverse observer groups, including developmental cohorts, patient populations, and persons with idiosyncratic oculomotor patterns. In control experiments with physically reversing image motion, ocular responses (i.e., reversal of smooth pursuit direction) detected by CSP exhibited significantly less temporal variability (approximately 55% smaller interquartile range) than ocular responses detected by existing methods (Naber et al., 2011; Frässle et al., 2014). During nearly linear pursuit episodes, CSP estimates proved approximately 15% more accurate than existing methods. In general, CSP analysis appeared to be marginally more sensitive and/or more volatile than existing methods, with estimates covering a slightly higher range of velocity, acceleration, and jerk.

We conclude that CSP offers significant improvements over existing methods of monitoring binocular rivalry by means of recording OKN.

Methods

Subjects

The present study was performed with several observer cohorts, including neurotypical children (n = 28, aged 12), adolescents (n = 19, aged 16), young adults (n = 30, average age 21), older adults (n = 12, age 60), individuals with borderline disorder ([BD]; n = 12, average age 27), and individual with autism spectrum disorder ([ASD]; n = 12, average age 28). In addition, a number of more demanding control experiments were performed with practiced psychophysical observers (two young men, six young women, average age 24).

All participants had normal or corrected-to-normal vision and were naive to the purposes of the experiment. All observers passed a stereoacuity test before participating in the experiment (Super Stereoacuity Timed Tester, by Stereo Optical Co., U.S. Patent No. 5,235,361, 1993). All participants or caregivers (in the case of children) provided informed written consent. For neurotypical observers, the study was approved by the Ethical Review Committee of the Institute of Psychology, Pazmany Peter Catholic University. For participants with ASD and borderline personality disorder, the study was approved by the Semmelweis University Regional and Institutional Committee of Science and Research Ethics.

The diagnostic status of participants with borderline personality disorder was assessed by the Hungarian version of the Structured Clinical Interview for the Diagnostic and Statistical Manual of Mental Disorders, fourth edition, Axis I and II disorders (Szádóczky, Unoka, & Rózsa, 2004; Szádóczky, Rózsa, & Unoka,
Nine of 12 participants with ASD were diagnosed by a trained psychiatrist. They underwent a general psychiatric examination and their parents were interviewed about early autism specific developmental parameters. All nine participants fulfilled the diagnostic criteria of ASD, including autism-specific signs between the critical ages of 4–5 years. Three of 12 participants in this group were recruited from a nonprofit organization (Aura Organization) assisting people with ASD. No detailed diagnostic information was available for these three participants (Szádóczky et al., 2004).

Experimental stimuli and protocol

Setup

Nearly identical setups for dichoptic stimulation and eye position recording were used in Magdeburg and in Budapest, as described previously (Pastukhov & Braun, 2010; Figure 1). Observers were fixated by a headrest and viewed the two displays through 45° mirrors, with each eye viewing a different display. The mirrors were coated to reflect visible light but to be transparent to infrared light, providing a clear field of view for the infrared camera that records eye position. Brascamp and Naber (2017) described a similar setup in detail.

Stimuli

The gratings moved horizontally, either leftward or rightward. From the observer’s point of view, the two gratings underwent uniform horizontal motion, either consistently (in the same direction) for the replay condition, or inconsistently (in opposite directions) for the rivalry condition. Each grating subtended a rectangular area of $15.2^\circ$ width and $8.4^\circ$ height. Spatial frequency was 0.26 cycles/° and temporal frequency 8.7 cycles/s horizontally. The speed of horizontal motion was $33.5^\circ/s$ or 1600 pix/s. To facilitate binocular fusion, gratings were framed by a rectangular box with a random texture pattern. Stimuli was generated with Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) running under MATLAB R2015a. The spatial resolution was 48 pix/°, and the temporal refresh rate was 120 Hz.

Protocol

The experiment with developmental and patient cohorts consisted of 10 trials of 95 s duration. The first trial served to familiarize observers with the display and was not included in the analysis. It comprised 20 s of consistent grating motion in alternating directions, 72 s of inconsistent motion (which induced rivalry), finishing with 3 s of consistent motion. The remaining nine trials consisted of 2 s of consistent motion, 92 s of inconsistent motion, and 1 s of consistent motion. The consistent episodes served to reduce eye strain and to test the ocular response to physical motion reversals.

The control experiments with experienced psychophysical observers consisted of six trials. A first familiarization trial lasted 30 s with consistent grating motion reversing every 3 s. A second passive viewing trial lasted 90 s with consistent grating motion reversing at random intervals sampled from a $\gamma$ distribution with mean $\mu = 3$ s and standard deviation $\sigma = 1.8$ s.

Under the passive conditions, observers were instructed to view the display as attentively as possible and to refrain from blinking as much as possible.

The four remaining active viewing trials lasted 90 s and included two replay and two rivalry trials. In replay trials, grating motion was always consistent and reversed at random intervals sampled from the $\gamma$ distribution describe above. In rivalry trials, grating motion was consistent for 2 s and inconsistent for the remaining 88 s of the trial. Replay and rivalry trials were presented in random order.

Under active conditions, observers were instructed additionally to report the apparent direction of motion by pressing one of two keys. Specifically, they were requested to report the initial apparent direction and any subsequent reversals of apparent direction by pressing the right- or left-arrow keys.
Eye movement analysis

Horizontal position of the left eye was recorded with an Eyelink 1000 (SR Research Ltd, Ottawa, Canada), with temporal sampling of 1 kHz. The analysis of recordings involved several steps. Briefly, fast and slow phases of horizontal OKN were identified and, after removing the former, the latter were interpolated into a continuous and cumulative record of smooth pursuit. Below, the principal steps are described in more detail.

 Artefact removal and extraction of slow OKN phases

Raw recordings are typically contaminated by blinking artefacts, in which nominal gaze position falls outside the display area. Such off-scale events were removed, together with the adjoining 50 ms on either side, from the recording.

To distinguish fast and slow segments of horizontal OKN, the recording was filtered bidirectionally with a 50-ms kernel. Specifically, a moving average was computed separately for 50-ms windows sliding forward and backward in time. The two moving averages were combined into a filtered record of eye positions. Absolute eye velocity \( |v| \) was computed numerically from successive position values. The velocity distribution was bimodal and the saddle point between the densities of low and high velocity was adopted as threshold criterion (1.5 pix/ms). Slow segments represented periods of smooth pursuit. Fast segments represented fast OKN phases, saccade-like eye movements, and occasional recording artefacts. Positive or negative eye acceleration \( a \) was computed from successive velocity values. The distribution of accelerations peaked symmetrically at zero acceleration, with the 5% and 95% quantiles observed at approximately \( \pm 0.12 \) pix/ms\(^2\), respectively.

Time segments of slow velocity \((|v| \leq 1.5 \) pix/ms\) and low acceleration \((|a| \leq 0.12 \) pix/ms\(^2\)) were retained, provided their duration exceeded 50 ms (Figure 2A, red traces). All other segments were disregarded (Figure 2A, gray traces).

Importantly, all subsequent analyses (including concatenation and interpolation) were based on retained time segments from the original, raw recording (rather than the bidirectionally filtered recording). Thus, the final result did not rely on filtered eye position records.

Continuous record of smooth pursuit

In the present context, eye velocity is in the center of interest, not absolute eye position. Accordingly, we shifted the absolute position of each segment vertically, such as to maintain continuity of both velocity and position, after shifting. Due to these positional shifts, absolute position was replaced by cumulative position. Specifically, given successive smooth pursuit segments \( x_1(t), t \in T_1, \) and \( x_2(t), t \in T_2, \) we joined these segments by fitting a four-parameter function \( f(t) \) (three-parameter parabola plus offset) to the final 50 ms of the earlier and the first 50 ms of the later segment:

\[
f(t) = \begin{cases} \frac{a_1 t^2 + b_1 t + c_1}{a_2 t^2 + b_2 t + c_2 - \text{offset}} & \text{if } t \in T_1 \\ \frac{a_1 t^2 + b_1 t + c_1}{a_2 t^2 + b_2 t + c_2 - \text{offset}} & \text{if } t \in T_2 \end{cases}
\]

Figure 2B shows a representative recording with unshifted segments (red curves) and shifted segments (blue curves) corresponding to the best parabolic fit. After shifting, the segments form a cumulative, but still intermittent, record of smooth pursuit (CSP). Note that positive CSP slope corresponds to rightward pursuit, negative slope to leftward pursuit.

To obtain a continuous estimate of positive or negative eye velocity \( v \), the disjoint segments of CSP were used as anchors for robust splining (i.e., repeated splining of random subsamples). Specifically, each recording was subsampled \( 10^3 \) times by a factor of 1/100 and splined with a shape-preserving, piecwise-cubic, Hermite-interpolating polynomial (Carlson & Fritsch, 1985). The splined subsamples were averaged and the time-derivative was computed numerically. The median and the 95% CI of estimated eye velocity are illustrated in Figure 2C (green trace and light green area). The same three quantiles (2.5%, 50%, and 97.5%) of the velocity distribution provided the basis for estimating perceived motion (see next section).

To summarize, the present approach (a) smooths raw observations in an adaptive manner (by robust splining), (b) interpolates gaps in a manner that avoids discontinuities in velocity (by splining), and (c) estimates local velocity and acceleration from a neighborhood (a splined segment).

Estimate of perceived motion

As horizontal smooth pursuit tends to follow perceived horizontal motion (Enoksson, 1963; Merrill & Stark, 1963; Frässle et al., 2014; Fujiwara et al., 2017), we inferred perceived motion from horizontal velocity of smooth eye movements. In principle, zero-crossings of horizontal eye velocity may indicate reversals of perceived motion. However, horizontal eye velocity may approach zero for several reasons other than a reversal of perceived motion, including slowing of pursuit, lapses of perception or attention, transitions from and to the same perceived motion (“return transition”), perception of mixed motion, and artefacts introduced by processing.
To distinguish conclusive from marginal zero-crossings, we used a gaze velocity threshold of ±0.1 pix/ms as an additional criterion (Figure 2C, gray). This value was a conservative choice, and larger values, up to approximately ±0.4 pix/ms, would have served equally well.

Conclusive transitions were defined in terms of the entire velocity confidence interval (from 2.5% to 97.5% quantiles) crossing either the upper threshold (from above or below) or the lower threshold (from above or below). The timing of such a conclusive transition was defined by the nearest threshold-crossing of mean velocity (green trace).
crossing of the 50% quantile. This approach defined both the beginning and the end of dominance phases and transition phases. It also allowed us to distinguish different kinds of transition phases, specifically, forward transitions leading to the opposite dominance as previously and return transitions leading to the same dominance as previously (see Figure 2, Insets I and III, respectively). Note that this approach rejects marginal transitions without resorting to a temporal criterion (see Figure 2, Inset II). Accordingly, the lower bound for dominance and transition durations is not set explicitly but implicitly by the confidence interval for velocity.

The precision of the determination of the beginning or ending of a transition phase was estimated individually for each threshold-crossing of the average spline. To this end, we computed the standard deviation of threshold-crossings (of the time-derivative of) individual splines around the threshold-crossing of the average spline. The resulting value was essentially the half-width of a 67% confidence interval.
To compare our results to existing methods, we implemented the algorithm of Frässle and colleagues (2014). To this end, eye velocity was computed numerically from successive values of horizontal eye position. High-frequency noise was suppressed by averaging over a 500-ms sliding temporal window. Gaps in the eye velocity record were interpolated linearly. To assess perceptual state, zero crossings in the filtered and interpolated eye velocity were determined. Specifically, zero crossings were retained only if separated by 400 ms or more. More closely spaced zero crossings were disregarded. Thus, 400 ms was the minimal duration of detected perceptual states.

**Statistical methods**

**Summary statistics**

Unless otherwise mentioned, we report grand means of data pooled from all observers, plus minus the standard error of the mean. Distributions were compared in terms of differences between medians and/or between interquartile ranges (IQR) or between 95% CIs (interquantile range from 2.5% to 97.5%).

**Combined distributions**

To highlight similarity of distributions obtained from different observers, it was sometimes useful to first normalize observations for each individual observer.

For example, we normalized CSP velocity distributions of individual observers by means of z scoring (normalizing to zero mean and unit variance), prior to pooling all observations in a combined distribution of velocity. Note that the low-velocity range ±0.1 pix/ms occupied a slightly different position for each observer in terms of z-score units.

Similarly, we normalized dominance durations to the individual observer mean $T_{dom}$, prior to pooling all observations in a combined distribution of dominance durations.

**Statistical tests**

To assess the statistical significance of differences between the medians of distributions of latencies or durations, we used the Wilcoxon rank-sum test.

To assess the statistical significance of differences between the proportions of return transitions, we used the z test for binomial distributions.

To assess the statistical significance of differences between interquantile ranges, we resorted to a boot-
strapping approach. The two original sets of samples were merged and randomly divided into two new sets. This sampling was repeated (>10⁴ times) and a distribution of interquantile ranges was established (null hypothesis). The significance of observed interquantile ranges was then assessed in terms of this null distribution.

**Violin plots**

To visualize the distributions of latencies and durations, we used “violin plots” implemented by the gramm MATLAB toolbox (Morel, 2018). These plots superimpose a normal box plot and a violin-shaped rendering of a distribution.

Box plots present the median ± interquartile range of the distribution. Notches were drawn at ±1.58 *IQR* /√N, where N is number of observations. The whiskers extend above and below the box to the most extreme data points that are within a distance to the box equal to 1.5 times the interquartile range (Tukey boxplot). Points outside the whisker range were plotted as outliers. The violin shape visualizes the probability density function and represents the distribution of samples. The thickness of the violin indicates how common (probable) a given sample value is.

**Results**

To assess the performance of the CSP analysis, we recorded eye position during binocular rivalry in 30 neurotypical observers of age 21 years and compared the results with existing analysis methods (Frässle et al., 2014). To assess the robustness of CSP for different populations, we also investigated 59 neurotypical observers of ages 12, 16, and 60 years, as well as a further 24 observers with BD or ASD. Note that statistical differences in binocular rivalry as experienced by different age and patient groups are not relevant in the present context and will be reported elsewhere.

To assess the reliability of CSP as an indicator of perceived motion, we compared volitional reports of perceived motion in two control experiments with an additional group of eight trained psychophysical observers. One experiment investigated ocular responses to physical reversals of image motion in nonrivalrous displays (replay condition) and the other ocular responses associated with spontaneous perceptual reversals induced by binocular rivalry displays (rivalry condition). Additionally, both experiments were performed under both active viewing conditions (i.e., with volitional reports) and passive viewing conditions (i.e., without such reports).

**Robustness of CSP analysis**

To assess the robustness of CSP analysis, we processed 983 eye position recordings of 90-s duration, from 113 neurotypical observers of different ages (12, 16, 21, and 60 years) and from 24 individuals with BD or ASD.

Eye movement records were analyzed in a fully automated fashion, as described in Methods. Four examples of rivalry recordings of different quality, all from healthy, 21-year-old observers, are illustrated in Figure 3. The original eye position record (red trace) including eye blinks (green overlay) is compared with CSP segments (blue traces). Positive CSP slope corresponds to rightward pursuit, negative slope to leftward pursuit. The quality of each record was assessed in terms of the relative proportion of identified smooth pursuit segments and of gaps between such segments. The fraction of the former ranged from 79% to 1%. Recordings with at least 50% identified smooth pursuit segments were included in further analyses, all other recordings were disregarded Figure 3E.

In our corpus of 983 recordings, 804 recordings (82%) exceeded the quality threshold. Of 113 observers, 99 observers (90%) produced recordings of acceptable quality at least half the time. The remaining 10% of observers exhibited unusually slow velocities of smooth pursuit, which were reduced more than 10-fold as compared with the other observers (Figure 3D). It is unclear whether this unusually low gain reflected measurement problems or genuine physiological deviations.

**Relative latency of CSP analysis**

To assess the reliability of CSP as an indicator of perceived motion, we compared reversals of smooth pursuit direction with reversals of physical image motion and with volitional reports of reversals of physical and/or perceived motion, using both healthy young adults and practiced psychophysical observers.

Under rivalry conditions, observers dichoptically viewed a rivalrous display, in which perceived motion reversed spontaneously at irregular times. Under replay conditions, observers binocularly viewed a nonrivalrous (i.e., unambiguous) display, in which image motion reversed physically at irregular times. Frequency and variability of reversal timing was comparable under both conditions (hence “replay”). Eye position records were analyzed as described above in terms of CSP. Reversals in the direction of smooth pursuit were interpreted as ocular responses to reversals of physical or perceived image motion.

In addition, observers produced volitional reports of perceived image motion. Specifically, observers were
instructed to press either a "motion left" or a "motion right" key, whenever the perceived motion changed. In the replay condition, ocular responses and volitional reports could also be compared with reversals of physical image motion.

In addition to an active viewing condition in which observers produced volitional reports, we also investigated a passive viewing condition in which observers simply viewed the display. Unsurprisingly, observers appeared to be somewhat less alert and attentive under passive viewing conditions (24 min, 718 reversals total). For rivalry and passive viewing conditions, we used part of the larger data set mentioned above (30 neurotypical observers of age 21–25 and 40,418 reversals total). A representative example of a recording with motion reversal, ocular response, and reported reversal of perceived motion (volitional report) is shown in Figure 4A. The latencies between the three types of events—motion reversal, ocular response, and reported reversal of perceived motion (volitional report)—are summarized in Figure 4B and C and in Table 1. When replay displays were viewed actively, reversals of image motion were followed almost invariably by a corresponding reversal of ocular motion (95%, latency < 1 s). Relative to motion reversals, the mean latency was lower for rivalry displays (85%).

Figure 5. Cumulative trajectories of smooth pursuit. Cumulative trajectories of smooth pursuit were temporally aligned to motion reversals (left column), ocular responses (middle column), and volitional reports (right column). Rising trajectories represent leftward motion (red icon), falling trajectories rightward motion (green icon). Average and standard deviation are shown separately for leftward-to-rightward and rightward-to-leftward reversals. (A) Active viewing of replay (red) or rivalry (gray) displays. (B) Passive viewing of replay (red) or rivalry (gray) displays.
significant (Figure 4B). The difference between medians was highly significant \( p < 10^{-3} \). The mean interval between ocular responses and volitional reports was 259 ± 48 ms. When the same display was viewed passively, the latency of ocular responses was 189 ± 9 ms, which did not differ significantly from active viewing.

The respective variability of ocular responses and volitional reports was quite different. Specifically, when replay displays were viewed actively, we obtained 95% interquantile ranges of 97.5 ms for ocular responses and of 151 ms for volitional reports. This difference was significant \( p < 0.05 \). The variability of intervals between ocular responses and volitional reports was 326 ms (95% interquantile range).

When rivalry displays were viewed actively, the mean interval between ocular responses and volitional reports was 400 ± 53 ms SEM (Figure 4C). Individual intervals were highly variable, with a 95% interquantile range of 393 ms. Both mean and variability of these intervals were significantly larger than for replay displays, as described above \( p < .01 \) and \( p < .001 \), respectively. There could be several possible reasons for this difference, including that reversals of perceived motion proceed more gradually and/or more variably than reversals of physical motion.

### Comparison to existing methods

To compare CSP results to existing methods (Naber et al., 2011; Frässlé et al., 2014), we reanalyzed our eye position recordings with the algorithm of Frässlé and colleagues (2014). For active viewing of replay displays, the latency of ocular responses (relative to motion reversal) detected by the two approaches was statistically indistinguishable, with a median of median 189 ms for CSP and 183 ms for Frässlé and colleagues. However, the variability of latencies was considerably smaller for CSP (interquartile range = 55 ms) than for the method of Frässlé and colleagues (interquartile range = 123 ms). The difference in variability was highly significant \( p < 10^{-6} \). Accordingly, CSP results were approximately 55% less variable than existing methods.

In a second comparison, we assessed to precision of eye movement estimates from CSP and from the algorithm of Frässlé and colleagues (2014). For this purpose, we focused on highly linear smooth pursuit episodes in our recordings from 30 neurotypical observers (age 21). For each such episode, we estimated true eye velocity as the slope of a fitted regression line (with \( r > 0.999 \)) and analyzed the distribution of residuals (difference between CSP velocity estimates and true velocity). For episode durations from 150 to 550 ms, average residuals ranged from 45 to 80 pix/ms \( (M = 56 \text{ pix/ms}) \). With the method of Frässlé and colleagues, average residuals ranged from 57 pix/ms to 82 pix/ms (mean 66 pix/ms). Although this difference was not large (approximately 15%), it was highly significant \( p < 10^{-6} \). Accordingly, even under ideal conditions of highly linear eye motion, CSP analysis further improves the precision of (already good) eye velocity estimates.

In a third comparison, we considered the distribution of absolute eye velocity \(|v|\), absolute acceleration \(|a|\), and absolute jerk \(|j|\) (change in acceleration), as estimated by CSP and by the algorithm of Frässlé and colleagues (2014) from 30 neurotypical observers (age 21). As described in Methods, the CSP analysis smoothed and interpolated the eye position record in an adaptive (context-dependent) manner. The median and interquartile range of the resulting distributions were 440 ± 230 pix/s for \(|v|\), 4850 ± 4125 pix/s² for \(|a|\), and 7.4 ± 6.7 \times 10^{5} \text{ pix/s}^3 for \(|j|\). In contrast, Frässlé and colleagues (2014) computed eye velocity numerically from successive position values and filtered the result in a non-adaptive (context-insensitive) manner. With this approach, the resulting median and interquartile range were 420 ± 210 for \(|v|\), 4500 ± 3600 for \(|a|\), and 5.0 ± 3.6 \times 10^{5} \text{ pix/s}^3 for \(|j|\), in the same units as above. Thus, the median of velocity, acceleration, and jerk from the CSP analysis was consistently higher (5%, 8%, and 25%, respectively), although the difference was significant only with respect to jerk \( p < 0.2, p < 0.1, p < 0.05 \), respectively.

We suspect that this difference reflects a (desirable) increase in the sensitivity of eye velocity estimates. However, we cannot rule out an (undesirable) increase in the volatility of estimates. Deciding the issue would require a situation in which true eye velocity was known.

### Trajectory of CSP

Before and after smooth pursuit reverses direction, the trajectory of CSP is rather stereotypical and consistent. These average trajectories are of interest, as
they track the progress of reversals of perceived motion under different conditions. Average CSP trajectories during pursuit reversal are illustrated in (Figure 5). To obtain this figure, we temporally aligned several hundred individual trajectories, recorded from eight practiced psychophysical observers, to obtain the mean eye position and its standard deviation, at different times before and after a reversal. During active viewing of a replay display, average CSP trajectories develop almost monotonically before and after reversals of image motion (motion reversal), pursuit direction (ocular response), and volitional report (red traces, Figure 5A). During active viewing of a rivalry display, average CSP trajectories are less consistent, presumably reflecting the more gradual nature of perceptual reversals (gray traces, Figure 5A). During passive viewing of replay displays, average trajectories again develop monotonically (red traces, Figure 5B). However, during passive viewing of rivalry displays, cumulative trajectories again become less consistent (gray traces, Figure 5B). It is possible that the greater variability of perceptual reversals is exacerbated by reduced alertness or attention under conditions of passive viewing.

To take a closer look at the apparent differences between replay and rivalry conditions (i.e., between reversals of physical and perceived motion), we compared the respective acceleration of CSP, before and after it reverses direction (Figure 6A). During physical reversals, acceleration peaks sharply at the precise moment of the reversal, falling to near zero within a quarter second before and after (red traces). In contrast, during perceptual reversals, acceleration rises and falls more gradually (gray traces). The difference in peak acceleration is highly significant ($p < .0001$, Figure 6B). We suspect that this difference may reflect the more gradual and variable nature of perceptual reversals. The extent to which cumulative pursuit can reveal the internal dynamics of perceptual reversals is discussed below.

To assess the consistency of CSP trajectories in different observer groups, we repeated the analysis separately for different age and patient groups. Qualitatively, almost all groups produced consistent results, with comparable pursuit velocities and accelerations before, during, and after perceptual reversal (Figure 7). The one exception was older observers (age 60), in whom pursuit velocity and acceleration were noticeably diminished.

**Phases of smooth pursuit**

The approach described here reveals considerable detail about different phases of smooth pursuit behavior. The distribution of CSP velocity consistently
exhibits two peaks for positive (rightward) and negative (leftward) pursuit, plus an intermediate peak at velocities near zero. The combined distribution from 30 healthy observers (age 21 years) is shown in Figure 8A, in z-score units (see Statistical methods). Clearly, pursuit velocity does not simply alternate between extended periods of positive or negative values, but also lingers for extended periods in a near-zero velocity regime.

Phases of strongly positive or negative pursuit velocity we term pursuit dominance, as they presumably correspond to phases of perceptual dominance of rightward or leftward motion, respectively. Phases of near-zero pursuit velocity we term ‘‘pursuit transition,’’ as they intervene between dominant phases. Which kinds of perceptual states correspond to such transition phases is at this point unclear and deserving of further study. Presumably, pursuit transitions overlap to some degree with the perceptual states sometimes described as mixed or patchy rivalry (Brascamp, Van Ee, Noest, Jacobs, & van den Berg, 2006; Pastukhov & Braun, 2011).

The parsing of CSP velocity into distinct phases of pursuit dominance and of pursuit transitions is illustrated (Figure 2C). Importantly, forward transitions (leading to the opposite dominance) and return transitions (leading to the same dominance) may also be distinguished. The approximate beginning and ending of such phases may be timed by comparing the confidence range of interpolated CSP velocity with a suitable low-velocity threshold (here ±0.1 pix/ms). The precision of this timing may also be estimated from the local CSP confidence range (see Methods). Overall, the average precision was approximately 50 ms (see also below).

The combined results from 30 healthy observers (age 21 years) are summarized in Figures 8B through E and 9. The observed pursuit dominance and pursuit transition durations were distributed approximately log-normally, as indicated by the approximately symmetric shape of their distribution on a logarithmic scale (Figure 8D). Dominance durations were far longer than transition durations. Note that, for these combined distributions, individual observer distributions were normalized to the individual average value of \( T_{\text{dom}} \) (see Statistical methods). Absolute values are given below.

Average duration of pursuit dominance was \( T_{\text{dom}} = 1.90 \pm 0.02 \) s (SEM). The average duration of forward pursuit transitions was \( T_{\text{forward}} = 230 \pm 20 \) ms, whereas the average duration of return pursuit transitions was \( T_{\text{return}} = 530 \pm 70 \) ms (Figure 8C). The beginning and ending of forward (pursuit) transitions was determined with a precision of 50 ± 1 ms (halfwidth of confidence interval). For return transitions, this value was 80 ± 3 ms (Figure 8C).

Trajectories of eye velocity during pursuit transitions are summarized in Figure 9. During long transitions, an extended period of constant low velocity is particularly evident (Figure 9AC). The extent to which velocity remains constant over all recorded transitions is visualized by plotting acceleration (i.e., velocity difference before and after the midpoint) against transition duration (Figure 9B and D). It is evident that, for transition durations over 200 ms, velocity typically remains nearly constant around the midpoint of the transition.

Are pursuit transitions a spurious phenomenon, due perhaps to temporary oculomotor indecision? Or do pursuit transitions reflect the dynamics of perceptual transition states, such as mixed or patchy percepts (Brascamp et al., 2006; Pastukhov & Braun, 2011)? To address these questions, we investigated...
the effect of perceptual adaptation on pursuit transitions, as this factor is known to interact with perceptual transitions (Pastukhov & Braun, 2011). To identify periods of comparatively weak or strong adaptation, we selected exceptionally short or long dominance periods $T_{dom}$ (where short and long were defined in terms of a 5% and a 95% quartile, respectively) (Figure 8B).

Return (pursuit) transitions were significantly more frequent immediately following short $T_{dom}$ (11.5% ± 1.0%) than immediately following long $T_{dom}$ (6.0% ± 0.9%). The overall probability of return (pursuit) transitions was 7.9% ± 0.9%. Both return and forward (pursuit) transitions were significantly longer immediately after short than after long $T_{dom}$ (Figure 8E). This effect was highly significant for forward (pursuit)
transitions (which were more frequent). In contrast, dominance phases were significantly shorter after short than after long $T_{dom}$, consistent with a positive sequential correlation.

These results mirror the known effects of perceptual adaptation on perceptual transition and dominance phases (see Discussion), suggesting that pursuit transitions may reflect the underlying dynamics of perceptual transitions.

**Discussion**

We have further improved an established “no-report” paradigm for monitoring the phenomenal appearance of binocular rivalry display without soliciting volitional reports from the observers (Naber et al., 2011; Frässle et al., 2014; Tsuchiya et al., 2015). Our improved analysis—CSP—has three main advantages: pursuit velocity is estimated continuously (not inter-
mittently); pursuit phases are discriminated with a temporal resolution better than ±100 ms; and performance is robust for a wide range of oculomotor patterns. Thus, our approach reveals additional details about the temporal progression of binocular rivalry and facilitates studies with developmental and patient cohorts.

Our results confirm and extend several conclusions from previous work (Naber et al., 2011; Kornmeier & Bach, 2012; Frässlé et al., 2014). A reversal of direction in physical display motion is followed by a reversal in smooth pursuit direction (an ocular response in our terms) with an average latency of approximately 200 ms. A manual motor response to the display reversal (volitional report) follows after a further delay of approximately 250 ms. Similarly, a reversal of apparent display motion is followed first by an ocular response and only approximately 250 ms later by a volitional report. An even larger lag (approximately 350 ms) has been observed between electrophysiological correlates of perceptual reversals and manual responses to such reversals (Kornmeier & Bach, 2012), albeit for multistable displays other than binocular rivalry.

A benefit of CSP is that pursuit velocity is estimated continuously (without intermittent gaps) and that confidence limits are provided at all times. This contrasts with existing methods (Naber et al., 2011; Frässlé et al., 2014), which produce an intermittent estimate without confidence limits. Where a ground truth may be established, CSP estimates were significantly less variable (55% smaller interquartile range of latencies) and more accurate (15% lower residual error), even under ideal conditions (highly linear pursuit episodes). Overall, CSP estimates ranged over marginally higher values of velocity, acceleration, and jerk (5%, 8%, and 25%, respectively), and thus appeared to be marginally more sensitive and/or marginally more volatile than existing methods.

The reason for these differences is algorithmic. Firstly, CSP filters eye position in an adaptive (context-sensitive) manner (i.e., by means of robust splining), whereas existing methods apply linear filtering, which is insensitive to context. Secondly, CSP interpolates gaps in the eye position record such as to avoid discontinuities in acceleration (again by means of splining), whereas existing methods introduce such discontinuities (by interpolating linearly). Thirdly, CSP estimates instantaneous velocity on the basis of an extended temporal neighborhood (i.e., by differentiating a robust spline), whereas existing methods compute velocity from a narrower basis (i.e., from two successive position values).

The phenomenal appearance of rivalry displays comprises not only the two categorical alternatives (i.e., leftward or rightward motion), but also intermittent or transitional appearances. These transitional appearances are of considerable interest, in part because they are thought to reveal the respective contributions to rivalry dynamics of adaptation and noise (Brascamp et al., 2006; Pastukhov & Braun, 2011). In studies of binocular rivalry, observers are therefore often asked to distinguish three categories of phenomenal appearance: leftward motion, rightward motion, and mixed/patchy motion.

Similar to phenomenal appearance, the velocity estimates of CSP exhibited a distinctly trimodal distribution (see Figure 8A). In addition to two modes for large rightward and leftward velocity, there was a third mode for near-zero velocities, suggesting that smooth pursuit did not merely alternate between rightward and leftward phases, but also lingered for extended periods at low velocities (see Figure 9). To quantify these phases of pursuit behavior, we parsed CSP records into periods of pursuit dominance (rightward or leftward velocity) and periods of pursuit transition (low velocity). The latter we subdivided into forward transitions (leading from one dominance to another) and return transitions (leading back to the same dominance). The temporal precision of this parsing was typically better than ±100 ms and reflected the local width of the confidence interval for pursuit velocity.

The succession of pursuit phases was fairly rapid, changing on average approximately once per second. Specifically, periods of pursuit dominance lasted approximately two seconds, return transitions averaged approximately half a second, and forward transitions approximately a quarter second. Accordingly, it was not feasible to establish and compare the associated perceptual dynamics from volitional reports.

Overall, the statistics of pursuit dominance phases resembled the results typically reported for perceptual dominance. Pursuit dominance phases conformed to an approximately log-normal distribution and exhibited a weakly positive sequential dependence, as expected for perceptual dominance phases (Murata, Matsu, Miyauchi, Kakita, & Yanagida, 2003; van Ee, 2009; Pastukhov & Braun, 2011; Cao, Braun, & Mattia, 2016).

In an effort to compare pursuit transitions with their perceptual counterparts, we investigated the effects of perceptual adaptation, which is known to affect the latter (Pastukhov & Braun, 2011). Specifically, at times at which adaptation is weak, perceptual transitions take longer and are more likely to return to the previous dominance than at other times. As a corollary, return transitions generally take longer than forward transitions. The presumed reason is that transitions are thought to be driven partly by adaptation (drift) and partly by noise (diffusion) (Kim, Grabowech, & Suzuki, 2006; Brascamp, van Ee, Noest, Jacobs, & Van
The results for pursuit transitions inferred from CSP records consistently mirrored results previously reported for perceptual transitions on the basis of volitional reports (Pastukhov & Braun, 2011). Firstly, return transitions (7.9% ± 0.9%) were less frequent than forward transitions (92.1% ± 0.9) and this proportion was almost identical to that reported previously for perceptual transitions (9% v. 91%) based on volitional reports. Secondly, return transitions took approximately twice as long as forward transitions, similar to the threefold difference observed previously for perceptual transitions. Thirdly, both forward and return transitions took significantly longer at times at which perceptual adaptation was weak, again consistent with previously reported results for perceptual transitions. These results are consistent with the possibility that oculomotor transitions closely reflect perceptual transitions.

We conclude that CSP improves existing methods for monitoring binocular rivalry by means of recording OKN (Naber et al., 2011; Frässle et al., 2014). By continuously estimating pursuit velocity within certain confidence limits, changes of oculomotor state may be detected with a precision better than ±100 ms. How closely and faithfully this reflects the underlying dynamics of perceptual states remains to be determined, but the results about forward and return transitions, summarized above, are encouraging in this regard. Being able to monitor binocular rivalry with higher temporal resolution may prove useful in several contexts, including the characterization of perceptual reversals, the validation of computational models of reversal dynamics, and the study of neurophysiological correlates of binocular rivalry.

**Source code repository**

The source code of the CSP analysis of eye position records is available free from the following repository: https://github.com/cognitive-biology/Cumulative-smooth-pursuit-analysis-of-BR-OKN

**Keywords:** optokinetic nystagmus, binocular rivalry, no-report paradigm, multistable perception

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**Footnote**

1 When adaptation is weak, driving forces are absolutely smaller and have relatively larger stochastic component, resulting in longer transitions and more uncertain outcomes.

**References**


